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# WATER REQUIREMENTS OF CERTAIN RODENTS FROM XERIC AND MESIC HABITATS

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## INTRODUCTION

MOST mammals require a daily supply of free water, although some desert forms are capable of existing with no source of water except that obtained from their food. The amount of water available in the habitats of the various kinds of mammals varies considerably. Furthermore, in certain seasons of the year, and especially in times of drought, the water available in certain habitats may be materially reduced. The water requirements of most forms undoubtedly are flexible enough to enable at least a part of each population to survive adverse periods. It is also to be expected that each form inhabiting a given region would have other adaptations related to water requirements which will enable it to survive any seasonal deficiency of the water supply.

This paper is concerned with two points: (1) the average water consumption of certain small rodents inhabiting xeric and moderately mesic climates, respectively, and (2) the ability of certain kinds of these rodents to survive a period of deficient water supply. The results of the experiments used to test these points are summarized in the present report; detailed records may be obtained from Lindeborg (1948).

I express my gratitude to Dr. Lee R. Dice of the University of Michigan for supervising my work and to Dr. W. F. Blair for many suggestions. To Dr. C. W. Cotterman, Dr. C. C. Craig, and Dr. Leo Katz. I am indebted for aid with the statistical analysis. The Laboratory of Vertebrate Biology of the University of Michigan supplied most of the equipment and stocks of mice. The completion of the study was supported in part by the Biological Science Department of Michigan State College, and Dr. H. R. Hunt of the Zoology Department of that college graciously furnished laboratory space.

## STOCKS OF ANIMALS

The several stocks of mice used in this study were secured at different times by L. R. Dice, W. F. Blair, W. H. Burt, M. A. Taylor, B. T. Ostenson, P. R. Sime, M. F. Landwer, and R. G. Lindeborg. The expeditions on which the stocks were collected were supported in part by the Carnegie Institution of Washington and in part by the Laboratory of Vertebrate Biology, the Museum of Zoology, and the Horace H. Rackham School of Graduate Studies of the University of Michigan.

The species and races of mice upon which observations were made are listed below. Scientific names are those of Miller (1923) unless otherwise stated.

Perognathus penicillatus eremicus. — Field-caught animals collected about 3 miles south of Alamogordo, Otero County, New Mexico.

Peromyscus eremicus eremicus. — Three stocks of laboratory-bred animals were tested. The mice used in the water-consumption determination of the eremicus — blandus series were collected near Lone Butte, about 13 miles west of Tularosa, Otero County, New Mexico. The mice utilized for a similar determination (Table II, Series 8) were collected 3 miles south of Alamogordo, Otero County, New Mexico. The stock tested in the water-deficiency experiment was collected 13 miles west of Oscuro, Lincoln County, New Mexico.

Peromyscus maniculatus gracilis. — The three stocks were collected in the Upper Peninsula of Michigan. Two of these originated in the Cusino State Game Area, Alger County: one stock was field-caught, the other laboratory-bred. The third stock, also field-caught, was collected near the town of Norway, Dickinson County, about 65 miles southwest of the Cusino area.

Peromyscus maniculatus rufinus. — Laboratory-bred animals. The parent stock was collected on the north side of Gyp Spring Canyon, 4 miles northeast of Capitan, Lincoln County, New Mexico.

Peromyscus maniculatus nebrascensis. — Laboratory-bred animals. The original stock was collected near Kennedy, 40 miles south of Valentine, Cherry County, Nebraska.

Peromyscus maniculatus bairdi. — Laboratory-bred mice. The parent stock was collected about 5 miles southwest of Fennville, Allegan County, Michigan.

Peromyscus maniculatus blandus. — Laboratory-bred mice. The original stock was taken about 3 miles south of Alamogordo, Otero County, New Mexico.

Peromyscus maniculatus exiguus (see Nelson and Goldman, 1932). — Laboratory-bred animals. The original stock was collected on San Martín Island, about 3 miles off the coast of Baja California (30° 29' N: 116° 07' W).

Peromyscus leucopus noveboracensis. — Field-caught animals from southern Michigan. Most of these were collected near Pinckney, Livingston County, but a few were taken near Ann Arbor, Washtenaw County.

Peromyscus leucopus tornillo. — Field-caught animals collected about 2 miles southwest of Alamogordo, Otero County, New Mexico.

Peromyscus truei truei. — Laboratory-bred mice. The original stock was trapped at Capitan Gap about 6 miles northeast of Capitan, Lincoln County, New Mexico.

Peromyscus comanche Blair (1943c). — The parent stock was collected on the slopes of Tule Canyon, about 12 miles northeast of Silvertown, Briscoe County, Texas (Panhandle section).

Microtus pennsylvanicus pennsylvanicus. — Field-caught voles trapped near Ann Arbor, Washtenaw County, Michigan.

## HABITATS OF FORMS

Most of the stocks of mice employed in this investigation live under one of two contrasting types of climate: (1) the semidesert climate of southern New Mexico and (2) the deciduous-forest-and-prairie climate of southern Michigan. Meteorological data for these two climatic types are summarized in Table I.

TABLE I

Meteorological Summaries for Alamogordo, New Mexico,
and for Ann Arbor, Michigan

From the United States Weather Bureau "Climatic Summary of the United States."

| | Alamogordo | Ann Arbor |
|---|---|---|
| Precipitation (in inches) | | |
| Mean annual | 10.92 | 31.35 |
| Months with more than one inch of rain | 4 | 12 |
| Months with less than one inch of rain | 8 | 0 |
| Months with more than two inches of rain | 0 | 10 |
| Temperature (Fahrenheit) | | |
| Mean annual | 61° | 47° |
| Lowest monthly mean temperature | 41.8° | 22.6° |
| Highest monthly mean temperature | 79.7° | 71.7° |
| Mean annual relative humidity (approximate) | 45% | 75% |
| Mean annual total snow (in inches) | 5.8 | 37.4 |

Southern New Mexico, in the region of Alamogordo, is characterized by slight precipitation, most of which falls in late summer. The 4 months with more than 1 inch of rain are July, August, September, and October. Periods of 70 consecutive days with less than 0.25 of an inch of rain may occur from March through September (Kincer, 1922). During 19 years, more than 30 periods of 30 consecutive days with less than 0.25 of an inch of rain have occurred.

In comparison with southern New Mexico, southern Michigan has a greater annual precipitation, which is evenly distributed throughout the year. Southern Michigan also has a lower mean annual temperature and a higher mean annual relative humidity. The 2 months with less than 2 inches of precipitation are January and February. Periods of from 42 to 49 consecutive days with less than 0.25 of an inch of rain have been known to occur between March and September, but in 19 years there have been only 12 periods of 30 consecutive days in which less than 0.25 of an inch of rain was recorded.

The types of vegetation that have developed under these 2 climatic regimes are also quite distinctive. The vegetation of southern New Mexico is sparse and xerophytic, except for the mountainous regions, which are forested. Dice (1942) subdivides the area into 4 major belts: the montane belt, the sabinal belt, the arid grassland belt, and the desert belt. The montane belt is discontinuous on mountain tops, where the characteristic tree is the yellow pine (Pinus ponderosa). The lower regions of this belt are made up of juniper and oak and are assigned to the oak-brush association. Below the montane belt is the sabinal belt, characterized mainly by the pinyon pine (Pinus edulis) and the sabino juniper (Juniperus monosperma). Along the sides of canyons and valleys a rocky-slope association frequently occurs, and the borders of the more permanent streams are assigned to the nogale association characterized by the nogale or walnut (Juglans major). A treeless area is frequent on the eastern slopes of the mountains and has been called the short-grass association. The arid grassland belt is at a lower level. It is missing on the western slopes of the Sacramento Mountains, where the desert belt extends upwards to meet the sabinal belt. The desert belt is at lower elevations and includes the desert plain and the lower desert slopes of the adjacent mountains. Four subdivisions of the desert plains are recognized in this area by Blair (1943a). Three of these (the creosote bush, mesquite, and atriplex associations) occupy broad belts lying parallel to the mountain front and are encountered in that order as one proceeds from the base of the mountains to the center of the Tularosa Basin. The fourth subdivision, the grassy-wash association, cuts across the other associations of the desert plain.

The vegetation of southern Michigan is largely mesophytic with a number of hydrophytic forms. The 2 main physiognomic types, grassland and forest, are discontinuous. Forested areas at ground level have slightly lower temperature, higher humidity, lower evaporation, less insolation, and less air movement than nonforested areas.

Five races of Peromyscus and one of Perognathus from the New Mexico area were tested. Descriptions of the areas where the mice were trapped are to be found in Dice (1930, 1940, and 1942) and Blair (1941, 1943a and 1943b). Peromyscus maniculatus rufinus is typical of the montane belt but occasionally it ranges also through the sabinal belt, avoiding the rocky slopes, and into the arid grassland. Peromyscus truei truei is most abundant among the rocks and cliffs in the sabinal belt; it ranges upwards into the rocky habitats of the yellow-pine association of the montane belt and sometimes extends down into the desert belt, where it has been taken with Peromyscus maniculatus blandus in the mesquite association and with P. leucopus tornillo in the grassy washes. Peromyscus eremicus eremicus lives mostly in rocky habitats of the desert and grassland belts. This species is associated with P. m. blandus in the mesquite and with P. l. tornillo (Blair, 1943a) in the grassy washes. Peromyscus maniculatus blandus inhabits a number of areas on the desert plains, but occurs in greatest abundance in the mesquite association and only rarely in the creosote bush and atriplex areas. This race ranges into the grassy washes, where it is found with P. leucopus tornillo. Tornillo is found characteristically in these washes but ranges occasionally into the mesquite and into the nogale associations. In the desert belt it seems to prefer the less arid habitats. Perognathus penicillatus eremicus is widely distributed on the desert plains and is most abundant in the mesquite, where it was taken with Peromyscus maniculatus blandus, and it is almost as abundant in the creosote-bush association, but uncommon in desert washes.

Peromyscus leucopus noveboracensis, P. maniculatus bairdi and one race of Microtus tested inhabit southern Michigan. P. l. noveboracensis, chosen to contrast with P. l. tornillo from New Mexico, lives in areas which are wooded or covered with heavy brush; certain individuals, however, have been taken several hundred yards from the woods in open grassland (Burt, 1940). P. m. bairdi, selected for comparison with P. m. blandus from New Mexico, is always found in well-drained open places, in fields, meadows, and pastures; it is especially abundant in the thickly matted and undisturbed grass along fence rows. It occurs sometimes in fields containing scattered shrubs but never in forests or thick brush. In fact, there is some evidence that its home ranges rarely if ever reach the edges of woods (Blair, 1940). Microtus pennsylvanicus pennsylvanicus occupies the poorly drained grasslands, meadows, and marshes. It is partial to moist ground and prefers rough meadows, where the grass is matted and dense, but may extend its range to higher ground during favorable conditions, receding again during dry weather.

Four other races of Peromyscus, representing several additional habitats were also tested. P. maniculatus gracilis occupies the same general habitats as P. l. noveboracensis, but in Michigan is confined to the northern part of the state. It is also found at times in open places, and commonly invades barns and hunting cabins and occasionally farm houses. P. m. nebrascensis is largely limited to the Sand Hills of western Nebraska. Precipitation in this area averages 23 inches per year, a status intermediate between the Alamogordo and Ann Arbor regions. The soil is loose and sandy with very little surface drainage. Surface soil is commonly dry as powder, but beneath the surface it is quite moist (Pool, 1912). The vegetation is sparse and characterized by bunch grass and Yucca glauca. Little is known of the life history of P. m. exiguus, which is restricted to San Martin Island. There is very little rainfall and no permanent water in its habitat (W. H. Burt, verbal communication). Nelson (1921) described the island briefly and stated that the entire surface is covered by extremely ragged and broken lava beds full of numerous pits, caves, jagged points, and sharp ridges. The lava is covered with an abundant growth of lichens. The most notable flowering plants are some cacti and Dudleya anthonyi. P. comanche (Blair, 1943c) was collected in western Texas and probably occupies a restricted range on the rocky cedar-covered slopes along the "break in the plains". This habitat is apparently somewhat less xeric than the Alamogordo region. The area from which this stock was taken is about 300 miles northeast of Alamogordo.

## LABORATORY CONDITIONS

The temperature in the combined stock and experimental room was regulated by a commercial type of room thermostat. Humidity was not controlled. Temperature readings were taken several times a day and wet-bulb and dry-bulb thermometer determinations at least once each day.

The mean temperatures for the various experiments ranged from 20.3 to 25.4° C. The lowest temperature recorded during the study was 16.4° C. which occurred only in one experiment. The next lowest temperature recorded was 19.4° C. In the Peromyscus experiments the maximum temperatures ranged from 23.1° to 26.8° C., except in one water-deficiency experiment in which the temperature reached 28.6° C. In an experiment with Perognathus 30° C. was reached. The mean relative humidities for the whole series of experiments ranged from 24 to 47 per cent.

## WATER CONSUMPTION BY NONBREEDING ADULT MICE

In order to determine whether the rate of water consumption by the several kinds of small rodents here studied were related to the availability of water in their habitats, the amounts of water drunk by representative individuals of the various races were measured under experimental conditions in which an abundant supply was constantly provided. The amounts of water consumed by more than 500 mice were measured for periods of 10 days or more. In all but 3 determinations (Table II, Series 6, 9, and 11), 10 male and 10 female mice of each of 2 different races were tested concomitantly. The number of mice in the remaining series was limited either by the number of mice or by the cages available at the time. The term "series" is here used to indicate all mice employed at one time in a given experiment; "stock" to designate all mice of a given race collected at a given locality and their descendants.

## Methods

The experimental wire-mesh cages, 9 x 15 x 8 inches, occupied a 5-tier rack, the shelves of which had been covered with about 1 inch of wood shavings. Each cage contained cotton, a small nesting chamber, a water bottle, and air-dry food (Dice, 1934). The mice were placed in individual cages in such an order that sexes and races alternated. The positions of the cages on the rack were changed midway in the experiment. At that time the lowest row, near the floor, was exchanged with the top row; the row next to the bottom was exchanged with the row next to the top; the middle row remained in position. The mice were weighed at the beginning, middle, and the end of each experimental period on a beam-type balance calibrated to 0.1 gram. The average of these figures was used as the weight of the mouse.

Distilled water was supplied to each experimental animal by an inverted test tube suspended through a hole in the top of the cage. The open end of the test tube had been heated over a flame until it was reduced to a diameter of about 2.5 mm. A bulge was blown at the closed end to prevent the tube from slipping through the hole. Up and down movements of the tube were prevented by placing a wire cap over the upper end of the tube. The cap was secured to the cage by means of a hinge on one side and a hook on the other. Sidewise movements of the lower tip of the tube, which might jar water from the tube, were prevented by inserting the lower end through an elliptical loop of wire fastened to the side of the cage. Several tests were made in which a mouse was placed in an experimental cage supported over a sheet of paper tinted with washable ink. Any drops of water on the paper left characteristic rings. The watering method was found to operate satisfactorily.

The water tubes were removed from the cage and filled by means of a burette calibrated to 0.1 cc. A fine auxiliary glass tip attached to the bottom of the burette made filling without spilling possible. Twenty additional water tubes were placed in holders on the side of the rack. The amount of water evaporated from these control tubes was measured weekly. At this time the control tubes were exchanged with an equal number of tubes from the experimental cages.

Mice were given at least a day to become accustomed to the new cages. The amount of water required to fill each tube was recorded daily, with few exceptions, for at least 10 days, averaged to a per-day basis, and corrected for evaporation. The time of day at which readings were taken varied somewhat, because day to day comparisons were not planned. The first and last readings of the series, however, were always made at the same time of day. When the tubes were filled they were changed from cage to cage in such a way that any one tube progressed along the rack alternating between races and sexes. Thus, each mouse drank from a different water tube each day, which compensated for any variations in water consumed that may have resulted from small variations in size of the opening in the tubes.

## Statistical Treatment

The statistical procedures used in analyzing the data from these experiments follow Snedecor (1946). The coefficient of correlation between the 2 variates measured, body weight and water consumed, was found not to be significant; consequently, treatment was confined to values of the amount of water consumed. Differences which are said to be "highly significant" denote the 1 per cent level of probability; those which are "significant" the 5 per cent level.

## Results

A summary, combining the data for males and females, of mean individual weights and of mean daily water consumption for each of the various series of Peromyscus tested is given in Table II, with standard deviations, coefficients of variation of water consumed, coefficients of correlation between body weight and water consumed, and two ratios: (1) water consumed per day per gram of body weight; (2) water consumed per day per square centimeter of body surface as computed from body weight.

Series 1 (Noveboracensis-bairdi). — Noveboracensis drank, on the average, 0.80 cc of water less per day than bairdi. Eight males and 8 females of this series were again tested 3 weeks later for a 12-day period, and in the replication noveboracensis drank an average of 0.86 cc less than bairdi. The difference between species in water consumption is highly significant in both determinations and the difference between trials is not. The same difference was later observed in a test of 8 noveboracensis and 9 bairdi over a 3-day period.

TABLE II

Data on Daily Water Consumption (When Supply is Unlimited) for Males and Females of Several Races of Peromyscus, Including Relation to Body Weight and Body Surface (As Computed from Body Weight)

Sigma = standard deviation, CV = coefficient of variation, r = correlation coefficient.

| Series | Race | Number of Mice | Body Weight | | Water Consumption | | | r | Ratio of Daily Water Consumption | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | Mean Individual Weight (gm) | Sigma (gm) | Mean Daily Amount (cc) | Sigma (cc) | CV (Per Cent) | | Per Gram of Body Weight | Per $cm^2$ of Body Surface |
| 1 | Noveboracensis† | 20 | 21.09 | 4.12 | 2.54 | .56 | 22 | .032 | .120 | .0391 |
| | bairdi | 20 | 18.72 | 2.88 | 3.34 | .93 | 28 | -.125 | .178 | .0557 |
| 2 | Tornillo† | 20 | 31.09 | 4.79 | 1.72 | .34 | 20 | .536 | .055 | .0204 |
| | blandus | 20 | 24.50 | 3.96 | 2.60 | .84 | 32 | .073 | .106 | .0363 |
| 3 | Noveboracensis† | 20 | 22.04 | 5.17 | 2.46 | .44 | 18 | -.325 | .112 | .0368 |
| | tornillo† | 20 | 27.70 | 6.29 | 1.99 | .60 | 30 | .294 | .072 | .0256 |
| 4 | Bairdi | 20 | 19.71 | 4.19 | 3.17 | .64 | 20 | .133 | .161 | .0511 |
| | blandus | 20 | 27.91 | 4.75 | 2.96 | 1.03 | 35 | -.010 | .106 | .0378 |
| 5 | Bairdi | 20 | 19.09 | 4.71 | 2.37 | .59 | 25 | .264 | .124 | .0390 |
| | nebrascensis | 20 | 21.42 | 6.22 | 2.02 | .45 | 22 | .159 | .094 | .0308 |
| 6 | Bairdi | 20 | 16.75 | 1.87 | 3.05 | 1.02 | 33 | .286 | .182 | .0548 |
| | rufinus | 13 | 23.72 | 6.44 | 2.39 | .89 | 37 | -.072 | .101 | .0341 |
| 7 | Blandus | 20 | 19.82 | 2.33 | 2.38 | .74 | 31 | .390 | .120 | .0382 |
| | eremicus | 20 | 21.09 | 2.40 | 2.86 | 1.05 | 37 | -.229 | .136 | .0441 |
| 8 | Eremicus | 20 | 21.42 | 2.61 | 1.85 | .52 | 29 | .271 | .086 | .0282 |
| 9 | Comanche | 18 | 22.61 | 2.55 | 3.55 | 1.13 | 32 | -.110 | .157 | .0475 |
| | nebrascensis | 18 | 17.89 | 3.15 | 1.82 | .49 | 27 | -.046 | .102 | .0313 |
| 10 | Truei | 20 | 32.40 | 6.11 | 2.77 | .88 | 32 | -.059 | .085 | .0321 |
| | exiguus | 20 | 23.78 | 5.00 | 3.05 | 1.06 | 35 | .173 | .128 | .0435 |
| 11 | Gracilis stocks | | | | | | | | | |
| | Cusino laboratory | 10 | 22.41 | 1.54 | 3.21 | .48 | 15 | -.133 | .143 | .0453 |
| | Cusino field | 10 | 17.56 | 1.86 | 1.71 | .55 | 32 | -.390 | .097 | .0298 |
| | Norway field | 10 | 24.50 | 5.63 | 2.72 | .56 | 21 | -.099 | .111 | .0379 |

† Field-caught mice.

Series 2 (Tornillo-blandus). — Blandus drank an average of 0.88 cc daily more than tornillo, a difference which is highly significant. This difference between species was also evident in a 3-day series in which 9 blandus and 8 tornillo were tested.

Series 3 (Noveboracensis-tornillo). — Noveboracensis drank 0.47 cc daily more than tornillo, a highly significant difference between races. A 3-day check on 8 mice of each species exhibited this same type of difference.

Series 4 (Bairdi-blandus). — Bairdi consumed 0.21 cc daily more than blandus. Later, when 3 males and 3 females were tested for 4 days, bairdi drank 0.24 cc more than blandus. Neither of these differences between races is significant. In a final test 9 mice of each race were tested for 3 days with no significant difference between races in water consumption.

Series 5 (Bairdi-nebrascensis). — Bairdi drank 0.35 cc per day more than nebrascensis, a significant difference. Later, a series of 9 females each of bairdi, nebrascensis, and tornillo was tested over a 14-day period. Daily water consumption averaged 2.47 cc for bairdi, 1.81 cc for nebrascensis, and 1.60 cc for tornillo. The only highly significant difference was one between species, that between bairdi and tornillo.

Series 6 (Bairdi-rufinus). — Bairdi drank 0.66 cc daily more than rufinus, a difference which is not significant.

Series 7 (Blandus-eremicus). — Blandus drank 0.48 cc per day less than eremicus, a nonsignificant difference.

Series 8 (Eremicus). — A different stock of eremicus, when tested by itself, consumed an average of 1.85 cc of water per day. A daily mean consumption of 1.79 cc was observed in a 6-day trial with 3 females of a third stock of this species.

Series 9 (Comanche-nebrascensis). — Comanche drank 1.73 cc per day more than nebrascensis. This difference is highly significant.

Series 10 (Truei-exiguus). — Truei did not differ significantly from exiguus. The latter species consumed 0.28 cc per day more than the former.

Series 11 (Gracilis stocks). — This test involved 3 stocks of the race P. m. gracilis. The Cusino laboratory stock drank 1.50 cc more than the Cusino field stock, and 0.49 cc more than the Norway field stock. The first difference is highly significant, the second just significant at the 5 per cent level. The Cusino field stock drank 1.01 cc less than the Norway field stock, a highly significant difference.

In addition to the numbered series of Peromyscus, water-consumption data were also obtained for Microtus and Perognathus.

Using the technique described for Peromyscus, a series of 5 males and 6 females of Microtus was tested for a 12-day period and was found to consume an average of 7.23 cc of water daily (from 4.75 to 10.85 cc). In this series the mean of initial and final body weights was 34.70 grams.

The technique for testing Perognathus was identical except that readings of water consumption were made at weekly intervals. A series of 6 males and 4 females of Perognathus were tested over an 8-week period. The average daily consumption of water in this series, after correction for evaporation loss, was 0.038 cc. Four individuals, however, apparently did not use any water at all. Of the two that drank consistently, one averaged 0.19 cc and the other 0.14 cc per day. One individual drank only for a 3-week period, averaging 0.19 cc daily; the remaining 3 were also sporadic, but averaged lesser amounts. Another series of 5 Perognathus of undetermined sex was tested during a 22-day period and found to average 0.20 cc per day (from 0.04 to 0. 51). When tested again over a 13-day period, this series averaged 0.18 cc daily (from 0.03 to 0.38). All of these mice apparently drank some water during each period.

## EFFECTS OF DEFICIENT WATER RATION ON BODY WEIGHT AND SURVIVAL

The experiments described above provide information about the amounts of water consumed by several races of rodents when a plentiful supply of water is available. Under this condition water consumption appeared to be highly variable. The question arose, therefore, as to whether the differences between the forms in amounts of water consumed were due to differences in their actual needs or merely to differences in individual preference or habit. In order to ascertain requirements for water in relation to survival, the following studies were made of 8 species and races of mice from habitats of various aridities.

Four of the stocks employed in these experiments originated in the semiarid climate of New Mexico and the other four in the more humid climate of Michigan. The semiarid area was represented by Peromyscus leucopus tornillo, P. maniculatus blandus, P. e. eremicus, and Perognathus penicillatus eremicus; the more humid area by Peromyscus leucopus noveboracensis, P. maniculatus bairdi, P. m. gracilis, and Microtus p. pennsylvanicus.

The effects of deficient water supply were studied by giving the mice progressively smaller daily amounts of water until death occurred. One experiment (Figure 1) compared the weight loss of 2 races of Peromyscus maniculatus, P. m. blandus from the semi-arid climate, and P. m. bairdi from the more humid climate, when subjected first to half rations and later to quarter rations of water. A second experiment compared the weight loss and survival time of individuals of 5 races of Peromyscus on reduced water rations (Tables III - V). A third experiment compared weight loss and survival time in 3 stocks of Peromyscus maniculatus gracilis on decreased water rations (Tables VI - VII). Studies were also made of the weight loss and survival time of specimens of Perognathus and Microtus under regimes of deficient water supply (Fig. 1).

## Methods

The equipment and techniques employed in the studies of normal water consumption described above were used in the experiments on the effects of a deficient water ration.

## Statistical Treatment

The effects of decreased water rations were evaluated by measuring the changes in body weight and by recording observations of survival time. These data were subjected to an analysis of covariance, as described by Snedecor (1946). Differences between adjusted means were tested for significance by Wishart's (1936) modification of the standard test. This modification desensitizes the test in proportion to the degree of difference between means of initial weights.

Because certain animals died during the experiments, plotting the average weights resulted in an erratic line. The use of percentage loss does not smooth the curve. To overcome this difficulty, a weight index has been employed. When a mouse died, the index weight of the remaining mice was obtained by the formula

$$B = \frac{A(W_2' + W_3' + W_4' + \dots\dots\dots W_n')}{(W_2 + W_3 + W_4 + \dots\dots\dots W_n)}$$

where A is the average weight of the mice at the weighing period preceding the death, B is the index weight, $W'$ is the individual weight at the weighing period following the death, and W is the individual weight prior to the death. Subscripts indicate the individual mice; $W_1$ would represent the mouse that died.

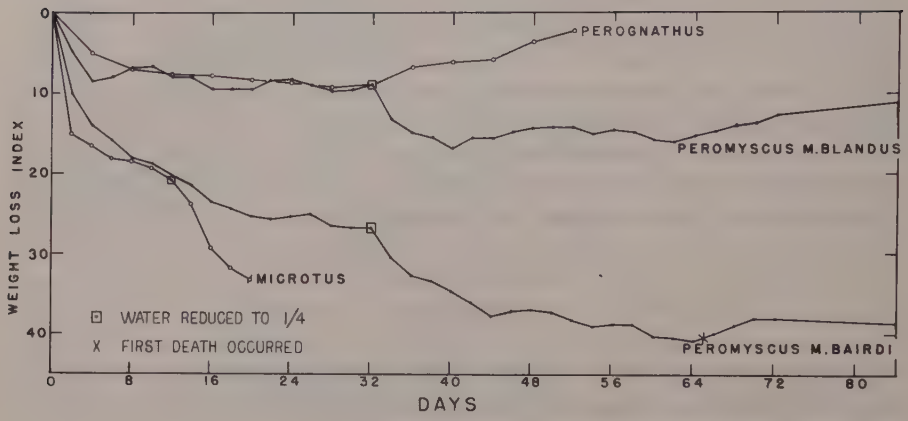

FIG. 1. Weight loss index of Perognathus, on no water, and of two Peromyscus races and of one race of Microtus, both on one-half and on one-quarter water ration.

⊡ Water reduced to one-quarter ration.

x First death occurred.

## Results

Experiment 1. The average voluntary water consumption of 3 males and 3 females each of Peromyscus maniculatus blandus and P. m. bairdi was determined, and then each mouse was given, for a period of 32 days, a daily ration equal to one-half its previous average consumption. After this, each individual was placed for 52 days on a further reduced ration, amounting to one-quarter normal consumption. The results, in terms of weight loss index, are presented graphically in Figure 1. In this and subsequent figures, the weight scale represents percentage loss up to the point at which the first death occurred, but thereafter becomes an index of weight lost. This point is marked by a cross on the line for each race. Also indicated are the days on which water was reduced.

The weight-index curves of Figure 1 indicate a similar physiological response on the part of blandus and bairdi to reduced water rations. When placed on half water rations, the mice at first lose weight rapidly, but the weight loss then tends to level off. Reduction of the ration to one-quarter normal results in further loss followed by slight gains. It is likely that some gain would also have been recorded on half rations had the mice been continued long enough on that regime. After 4 days on half rations, blandus showed a stabilization of weight with only moderate daily fluctuations thereafter; the final weight of blandus after 32 days on half rations was only slightly lower than that attained after 4 days. Bairdi lost weight over a longer period, at first more rapidly than blandus, then at a slower rate, and finally leveled off after a weight loss greater than that suffered by blandus.

In this first experiment (Fig. 1), the normal daily water ration was 2.66 cc for bairdi and 2.46 cc for blandus. When first placed on half ration, the average body weight for bairdi was 23.00 grams and for blandus was 21.58 grams. After 32 days on half ration, the mean weight for bairdi was 16.88 grams and that for blandus was 19.70 grams, indicating a weight loss of 27 per cent for the former and 9 per cent for the latter. Following the shift to quarter ration further loss in weight occurred, amounting on the average to 3.08 grams for bairdi and 1.90 grams for blandus. The difference between initial and final weights represents a loss of 37 per cent for bairdi and 10 per cent for blandus.

At the half water ration, the partial correlation between the amount of water consumed and the weight lost independent of initial weight was +.028 and that between water consumed and initial weight independent of weight lost was + .074. Neither of these values is a significant one. Evidently no particular advantage is gained by giving each mouse a specified fraction of its voluntary water consumption. In subsequent experiments, therefore, a uniform subminimal ration was given to each individual.

The variability in initial weights among individuals of both races is not markedly different from that in final weights. The coefficient of variation of initial weights was 17 per cent for bairdi and 21 per cent for blandus; that of final weights was 13 per cent for bairdi and 14 per cent for blandus. The partial correlation between initial weight and final weight, independent of water consumed, was +.967, a highly significant value. The final weight of an individual mouse is is evidently conditioned by its beginning weight. It is apparent, therefore, that the actual difference, 2.82 grams, between the mean weights of bairdi and blandus, after 32 days on half ration, does not give a very accurate measure of racial difference. The effect of initial weight can be controlled by use of the regression equation, whereby the final weights are adjusted to a uniform initial weight, and the differences between adjusted final weights can be tested for significance. The individual race regressions were not significantly different from the mean regression of both races and, consequently, the average regression was used in obtaining the adjusted means.

With an initial adjusted weight of 22.29 grams, the adjusted mean weight after 32 days on half water ration was 16.57 grams for bairdi and 20.01 grams for blandus. The difference of 3.44 grams between the 2 races is highly significant. The adjusted mean weight after 32 days on quarter ration was 13.14 grams for bairdi and 18.74 grams for blandus, giving an adjusted total weight loss of 9.15 grams for bairdi and 3.55 grams for blandus. The difference in total weight loss is highly significant.

Experiment 2. Five races of Peromyscus were placed on reduced water rations. Three males and 3 females each of Peromyscus leucopus noveboracensis, P. l. tornillo, P. maniculatus bairdi, P. m. blandus, and P. e. eremicus received a deficient supply of water for an extended period during which they were weighed at 2-day intervals. The groups, in the order named, while started at different times, were run concomitantly throughout most of the experiment. No abnormal fluctuations in the laboratory environment were noted during the 3 weeks in which the various groups were started; hence, it is believed that the lack of a common date of origin did not introduce any appreciable error into the experiment.

The average daily normal consumption of water for the mice used in this experiment was as follows: noveboracensis, 2.4 cc; tornillo, 2.0 cc; bairdi, 3.8 cc; blandus, 3.2 cc; and eremicus, 1.8 cc. In order to avoid a large initial reduction for the races of leucopus and maniculatus, which normally drink more water than eremicus, these forms were placed on half rations for several days. Later, the water ration was reduced to 0.9 cc, followed by reduction to 0.4 cc, then to 0.2 cc, and finally to no water at all.

The mean-weight index obtained in this experiment, together with the times at which the reductions in water ration were made, are shown graphically in Figure 2. It is apparent that the general trends duplicate those of the preceding experiment. The weight-loss curve drops rapidly at first and then levels off. Evidence of this trend is noted at each water-ration level for all races except noveboracensis, which was unable to adjust to the 0.2 cc ration. The races differ in their ability to adjust to reduced amounts of water, as indicated by differences in mean final weights on each water ration, by the curvature of the weight-index lines, and by the differences in weight gain after the initial loss.

Correlations between initial weight and final weight on each water ration are as follows: +.758 on half ration; +.814 on 0.9 cc; +.653 on 0.4 cc; and +.654 on 0.2 cc. These values are all highly significant. It was necessary, therefore, to make adjustments for differences in initial weights, as in the previous experiment. The mean final weights, adjusted to a mean initial weight of 23.77 grams, at each water ration are given in Table III and the differences between the adjusted means for the 0.9 cc ration are listed in Table IV.

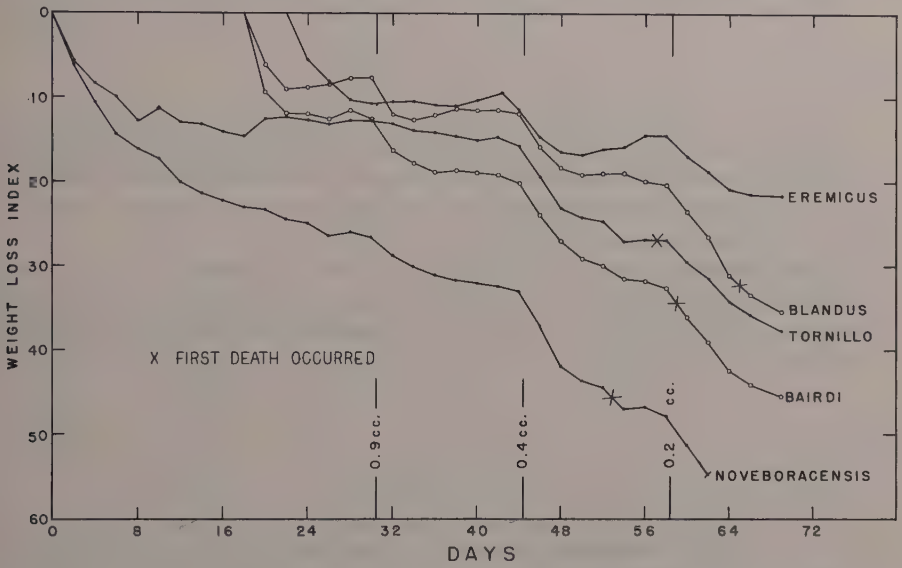

FIG. 2. Weight loss index of five races of Peromyscus on reduced water rations.

One-half ration for eremicus amounted to 0.9 cc and no change was made until all races received 0.4 cc water ration.

x First death occurred.

On half water ration the differences in adjusted mean final weights between noveboracensis and the other races were highly significant. In each comparison noveboracensis weighed less. Differences between the remaining races were not significant.

At the end of the 0.9 cc daily water-ration period, noveboracensis also weighed significantly less than the other races. Bairdi weighed significantly less than blandus or eremicus, but the differences in body weight between the other races were not significant.

TABLE III

Mean Final Individual Weights For Five Races of Peromyscus Adjusted to a Mean Initial Weight of 23.77 Grams

| Race | Mean Final Weight (in gm) on Daily Water Ration of | | | |
|---|---|---|---|---|
| | One-half | 0.9 cc | 0.4 cc | 0.2 cc |
| Bairdi . . . . . . . . | 20.15 | 18.51 | 15.70 | 13.62 |
| Blandus . . . . . . . | 22.12 | 21.10 | 19.05 | 16.58 |
| Noveboracensis . . | 17.56 | 15.96 | 12.58 | . . . . |
| Tornillo . . . . . . . | 21.16 | 20.40 | 18.32 | 15.92 |
| Eremicus . . . . . . | 20.82 | 20.80 | 20.04 | 18.33 |

Differences on 0.4 cc of water daily diverged from differences at 0.9 cc in only 2 respects. The bairdi-blandus difference was significant at the 2 per cent level and the bairdi-eremicus difference was significant at the 1 per cent level.

Differences between adjusted mean final weights on 0.2 cc water daily were not significant. By this time more than one-third of the mice had died, and the reliability of the test is questionable. Nevertheless, as shown in Figure 2, subjection to this low water ration

TABLE IV

Differences in Adjusted Mean Final Weights of the Five Races of Peromyscus on a Daily Water Ration of 0.9 cc

| Race | Difference (in gm) in Adjusted Mean Final Weight | | | |
|---|---|---|---|---|
| | Bairdi | Blandus | Noveboracensis | Tornillo |
| Blandus . . . . . . . | +2.59* | . . . . | . . . . | . . . . |
| Noveboracensis . . | -2.55* | -5.14** | . . . . | . . . . |
| Tornillo . . . . . . . | +1.89 | -0.70 | +4.44** | . . . . |
| Eremicus . . . . . . | +2.29* | -0.30 | +4.84** | 0.40 |

*Significant (5 per cent level).

**Highly significant (1 per cent level).

Plus or minus signs indicate whether the difference between the races is more or less than the one with which it is compared; that is, blandus weighed 2.59 grams more than bairdi; noveboracensis, 2.55 grams less.

accentuated the differences between races in all instances except that of the blandus-tornillo comparison.

The variability in final weights on 0.2 cc of water was similar to that in weights at the beginning of the experiment. The coefficient of variation of initial weights for the different races ranged from 6 to 26 per cent, and that of final weights from 14 to 24 per cent. On the basis of adjusted mean final weights on the 0.2 cc ration, eremicus lost 23 per cent of its weight in the course of the experiment, blandus lost 30 per cent, tornillo lost 33 per cent, and bairdi lost 43 per cent. The 3 noveboracensis which survived for only 3 days on this ration lost an average of 53 per cent of their initial weight.

TABLE V

Means of Initial Weight, Weight Loss, and Survival Days (with the Extremes) of Individuals of Five Races of Peromyscus on Various Water Rations

| Race | Mean Initial Weight (in gm) | Mean Weight Loss (in gm) on Daily Water Ration of | | | Survival Data | | |
|---|---|---|---|---|---|---|---|
| | | 0.9 cc | 0.4 cc | 0.2 cc | Mean of Days Lived | Days to First Death | Days to Last Death |
| Noveboracensis | 25.27 | 8.35 | 12.07 | . . . | 17 | 9 | 19 |
| Bairdi . . . . . . | 20.97 | 4.21 | 6.87 | 9.17 | 24 | 17 | 30 |
| Tornillo . . . . . | 25.60 | 4.03 | 6.66 | 9.72 | 28 | 13 | 39 |
| Blandus . . . . . | 24.32 | 2.87 | 4.95 | 7.30 | 29 | 21 | 42 |
| Eremicus . . . . | 22.68 | 2.58 | 3.26 | 4.91 | 41 | 34 | 44# |

# Three mice still alive.

Probably the best criterion for evaluating the effect of reduced water ration is the length of time a mouse can survive on it. Average initial weights, weight losses, and survival days of these 5 races of Peromyscus are given in Table V. Because the mice were started in the experiment at different times, total survival days cannot be used as a basis of comparison. However, the period on 0.4 cc of water daily and the subsequent period on 0.2 cc were of equal duration for all races. Since all of the mice apparently reached a stable weight on 0.9 cc daily of water, it is believed to be a proper reference point from which survival time can be counted.

Eremicus survived an average of 41 days after the water ration was reduced to 0.4 cc daily. This was the longest survival time and the differences between it and all other races are highly significant. Three eremicus died, before the experiment was closed, after 44 days on this ration, and the 3 remaining mice were given water thereafter. Forty-four days is, therefore, used as the survival time for these individuals in computing the mean for this race.

Noveboracensis was least well able to survive and lived an average of 17 days after the daily ration of water was reduced to 0.4 cc. The differences between it and the other races are highly significant, except for the comparison with bairdi, which is significant at the 5 per cent level.

Bairdi survived an average of 24 days on 0.4 cc water ration, tornillo 28 days, and blandus 29 days. Differences in survival time between these races are not significant.

Series of both Microtus pennsylvanicus and Perognathus penicillatus were also tested on a deficient water supply in this second experiment. Six male Microtus were placed in separate cages and each was given 3.4 cc of water daily, one-half their average normal consumption, for a period of 12 days. This was followed by a further reduction to 1.8 cc daily for an additional 10 days. Throughout both periods the mice were weighed at 2-day intervals. The results are shown graphically in Figure 1.

The weight-loss curve, though not complete, indicates a trend like that of Peromyscus, particularly bairdi, but at a slightly lower level. On half water ration, most of the loss occurs during the first 4 days, and the weight loss tends to level off thereafter. Following this initial loss, some weight gain was observed; 3 individuals gained an average of 0.61 grams from their lowest weights. On 1.8 cc of water daily the curve was similar except that no gains in weight followed the initial loss. In this experiment the mean survival time for Microtus was 18 days, with the first death occurring after 9 days and the last after 22 days. The 3 individuals which survived the experiment died within 2 days after all water was removed.

Three males and 3 females of Perognathus were confined in separate cages and fed the same type of food used for Peromyscus bue given no water. These mice were weighed every 4 days. Figure 1 also indicates the trend of weight loss and gain in this series. The mean weight of the Perognathus decreased for 28 days, most rapidly during the first 8 days, and then gains in weight were made for 24 days. One male gained throughout the experiment, and the mean final weight of the others was only 3.6 per cent below their initial mean weight. Perognathus was able to survive at least 52 days without water, and 2 individuals were kept on this regime for 81 days each without any apparent harmful effects.

Experiment 3. Three stocks of Peromyscus maniculatus gracilis were tested on deficient water rations. The decrease from normal consumption to 0.9 cc daily was made in one step, followed by further reductions to 0.4 and 0.2 cc, respectively. The 0.9 and 0.4 cc ration were maintained for 22 days each, and the 0.2 cc period lasted 32 days. All except one mouse died on the 0.2 cc ration, and this individual received water when it appeared likely to succumb if the experiment were continued. Weights were taken daily during the first week and every 2 days thereafter, except for the last few weighings, which were made at 3-day intervals. Weight trends are shown graphically in Figure 3.

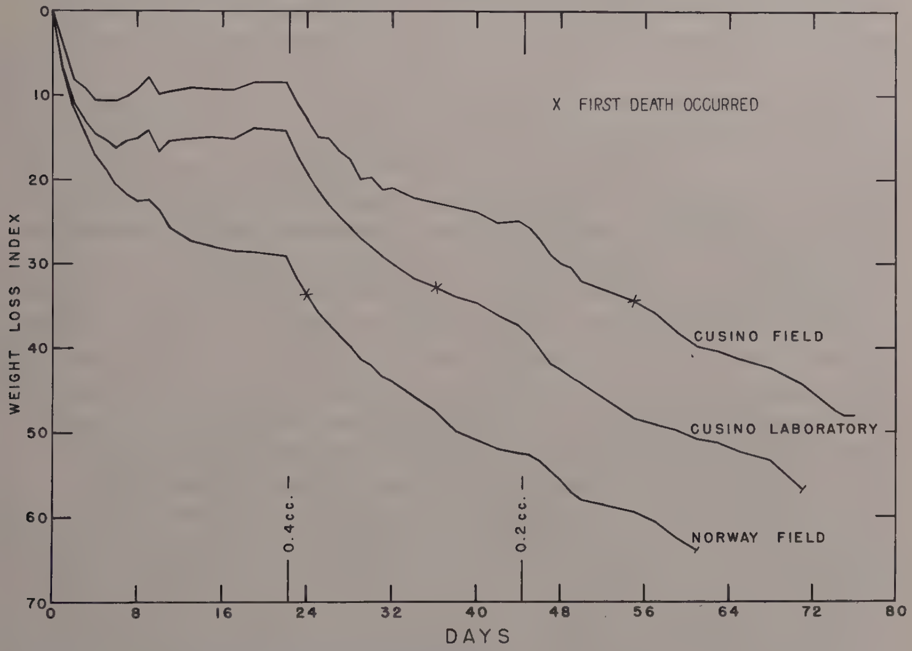

FIG. 3. Weight loss index of three stocks of Peromyscus m. gracilis on reduced water rations of specified daily amounts.

x First death occurred.

Weight changes were very much like those of the preceding experiments. The single-step reduction of water to a 0.9 cc ration increased somewhat the rate of weight loss but was not seriously detrimental to the mice. Both the Cusino field-caught stock and the Cusino laboratory-bred stock were able to stabilize their weights at a lower level, and the curve of Figure 3 suggests that the Norway field-caught stock might have done so had it been given more time. On the 0.4 cc ration, the tendency to stabilize weight was evident only in the Cusino field stock, and it was not appreciably

TABLE VI

Mean Final Weights of Three Stocks of Peromyscus m. gracilis
Adjusted to an Initial Mean Weight of 23.77 Grams, with Differences and Significance
at the 0.9 cc Water-ration Level

| Stock | Mean Final Weight (in gm) on Daily Water Ration of | | Weight Difference (in gm) on 0.9 cc Daily Water Ration | |
|---|---|---|---|---|
| | 0.9 cc | 0.4 cc | Cusino Laboratory | Norway Field |
| Cusino laboratory. . | 18.32 | 13.92 | | |
| Norway field . . . . . | 15.54 | 13.93# | 2.78** | . . . . |
| Cusino field . . . . . | 17.79 | 14.14 | 0.53 | 2.25** |

**Highly significant (1 per cent level).
#Only two mice were alive.

noticeable on the 0.2 ration. When placed on this lowest ration, loss in weight took place at an almost uniform rate until death occurred. None of the individuals was able to gain weight after initial losses.

The coefficient of variation in initial weights ranged from 7 to 21 per cent, that in final weights on 0.9 cc daily from 11 to 14 per cent, and that in final weights on 0.4 cc daily from 8 to 11 per cent. The mean final weights on the 0.9 cc ration, adjusted to a mean initial weight of 23.77 grams (identical with that used in Experiment 2), and the differences between them are shown in Table VI.

The correlation +.709 between initial and final weights on 0.9 cc of water daily is highly significant. At the end of this period, both

TABLE VII

Means of Initial Weight, Weight Loss, and Survival Days (with the Extremes)
of Individuals of Three Stocks of Peromyscus m. gracilis on Various Water Rations

| Stock | Mean Initial Weight (in gm) | Mean Weight Loss (in gm) on Daily Water Ration of | | | Survival Data | | |
|---|---|---|---|---|---|---|---|
| | | 0.9 cc | 0.4 cc | 0.2 cc | Mean of Days Lived | Days to First Death | Days to Last Death |
| Cusino laboratory. . . | 21.66 | 3.06 | 7.61 | . . . . | 49 | 35 | 71 |
| Cusino field . . . . . . | 18.04 | 1.51 | 4.49 | . . . . | 64 | 50 | 75# |
| Norway field . . . . . . | 23.31 | 6.79 | 7.75 | . . . . | 39 | 24 | 62 |

#One mouse was still alive.

of the Cusino stocks were significantly heavier than the Norway stock, but the difference between the Cusino field and the Cusino laboratory stocks was not significant. The adjusted final weights on the 0.4 cc water ration are not significantly different.

Table VII presents the data on initial weights, weight losses, and survival times of these 3 gracilis stocks. Unfortunately, no reference point is available for comparison with the 5 Peromyscus races tested in Experiment 2. The mean weight loss of the Norway field stock on the 0.4 cc ration is based on the records of the 2 individuals which survived this period; since these were from the top of this stock's weight range, the value of 7.75 is somewhat low. The mean survival time of the Cusino field stock includes a figure of 75 days for one individual that was given water after that time. On these reduced water rations, the Cusino field stock survived 15 days longer than the laboratory stock from the same area and 25 days longer than the Norway field stock from about 65 miles away. These differences are highly significant. The difference in survival time between the Cusino laboratory stock and the Norway field stock is significant at the 5 per cent level. None of these gracilis stocks was able to survive on 0.2 cc of water daily, in this resembling noveboracensis. From an inspection of Table VII it appears that the mice which lose weight most slowly survive the longer.

## DIFFERENCES IN WATER REQUIREMENTS OF MICE FROM HUMID AND FROM XERIC HABITATS

Although it has long been known that the water requirements of certain animals have a definite relation to survival, especially in xeric habitats, few critical studies of the water requirements of the smaller mammals have previously been made. In a study of the food and water requirements at various temperatures and humidities of Microtus ochrogaster, Peromyscus leucopus, and P. maniculatus, Dice (1922) failed to find differences between the water needs of the 2 Peromyscus species sufficient to be the basis of habitat preference within the same climatic area. Ross (1930) studied the comparative water intake of 5 races of laboratory-bred Peromyscus belonging to the species maniculatus and eremicus. When comparisons were made on the basis of water consumed per gram of body weight, significant differences were reported between species but not between races of the same species. Ross concluded that the races P. m. gambeli, P. m. rubidus, P. m. sonoriensis,

P. e. eremicus, and P. e. fraterculus had not diverged sufficiently in their evolutionary development to display differences that could be detected with the techniques he used.

Of fundamental importance in the study of water requirements of animals from different habitats is the basis of comparison. Shall the water consumed by the different animals be compared in terms of water consumption per individual, or in terms of water consumption per gram of body weight, or in terms of water consumption per unit surface area? In a study of water intake in the rat Richter and Brailey (1929) used as their measure of comparison the water consumed per unit of body surface area. Surface area is generally not measured directly, but is calculated from a formula in which the surface area is equal to a constant times the two-thirds power of the weight. In the present study several trial computations of surface area were made, using (a) the constant 8.5 for Peromyscus as reported by Pearson (1947) and (b) the constant of 9.1 used by Richter and Brailey (1929) for the rat. In no instance was the computed surface area found to be significantly correlated with the quantity of water consumed.

Water consumed per gram of body weight was employed in the studies of Dice (1922) and Ross (1930). The ratio of water consumed per gram of body weight was not employed as a basis of comparison in the present study, because in the analysis of covariance the regressions that were used involved weight and water as the variates. Correlations between body weight and water consumed were computed for each of the series of paired observations shown in Table II, for the races within each series, and for the sexes of each race. None of the correlations was significant at the 1 per cent level, and the number significant at the 5 per cent level did not deviate greatly from the expected occurrence of one in 20 trials. Replications showed considerable inconsistency. It was therefore assumed that in these instances body weight and water consumed were not correlated to any marked degree. This is apparently not true, however, of young individuals which are actively growing. Lindeborg (1950) found that water consumption increases with weight in growing young of Peromyscus maniculatus bairdi; Richter and Brailey (1929) discovered a similar trend in growing white rats.

Sex differences likewise had no discernible effect upon water consumption. Each of the series of observations recorded in Table II extended over at least 1 and in many cases over 2 estrous periods (Clark, 1936), and any differences in water consumption between males and females due to modified physiology during these periods should have been reflected in the data. For the 22 male : female comparisons available, only twice were the differences significant.

Since these differences might have been due to random sampling, it was concluded that males and nonbreeding females did not differ in amounts of water consumed.

Dice (1922) and Ross (1930) also considered the amount of water consumed per individual. In the present study the amounts of water consumed by individual mice in successive determinations about a month apart were measured for 3 races of Peromyscus. There were no significant differences between the determinations of the various individuals. Evidently the average amounts of water consumed by an individual under constant conditions remains quite consistent. Differences in the mean consumption per individual are thought to be a satisfactory basis for making comparisons.

The most striking differences in daily water consumption were those between genera of mice inhabiting different geographic areas. As already noted, the Michigan specimens of Microtus averaged 7.23 cc of water daily, in contrast to the mean of 0.038 cc consumed per day be those of Perognathus from New Mexico. The several species and races of Peromyscus were all intermediate between these two, so far as consumption of water is concerned.

The amounts of water consumed by the various species of Peromyscus from different habitats within the same climatic region were not conclusively different. A comparison of races from different geographic areas yielded highly significant differences between noveboracensis from Michigan and tornillo from New Mexico (at the 1 per cent level) and a significant difference between bairdi from Michigan and nebrascensis from the Sand Hills of Nebraska, but there were no significant differences between Michigan bairdi and either blandus or rufinus from New Mexico, or between truei from New Mexico and exiguus from San Martin Island. Mice originating in areas with more mesophytic vegetation apparently drink more water than those from primarily xerophytic regions. In seeming exception to this statement, comanche from western Texas drank more than nebrascensis, but it is quite possible that the amount of water actually available to these mice in their respective habitats may not be accurately reflected by known data.

Significant differences were also found between 2 stocks of the same race originating in the same climatic area. The Norway stock of gracilis from Michigan consumed significantly more water daily than the Cusino stock.

The differences noted above are all differences in voluntary water consumption. Voluntary consumption of water varied a great deal between individuals of all the races studied, and there was considerable overlap of measurements in each series. Conclusions based solely on differences in the amounts of water consumed voluntarily by various races of Peromyscus are not very reliable for the estimate of water needs in nature. Nevertheless, these experiments do show that, however inadequate voluntary water consumption may be as a basis of comparison, it definitely supports results obtained from the study of other aspects of water metabolism.

One of the other aspects of water metabolism studied was the response to a deficient supply of water. When the water ration of the various races was decreased to one half that voluntarily consumed, the mice lost weight, rapidly at first and more slowly later, until a weight level was reached beyond which no further loss occurred. If sufficient time is allowed on a reduced ration, the mouse may regain some or all of the weight lost. This suggests that the mouse becomes physiologically adjusted to the water deficiency. If further reductions in water ration are made, a similar response is usually evident. Reduction may reach a point, however, at which the mice are no longer able to adjust their physiological requirements to the amount of water received, in which case they lose weight steadily and soon die. The rate at which weight is lost apparently depends upon the amount of water provided and upon the species and race of mouse. The weight level maintained on any given water ration and the total survival time depend on these same factors and also on the length of time the mice have been held on the various rations.

The ability to regain eventually some of the initial weight lost after a reduction in water ration is apparently possessed by some races and not by others. This subsequent gain of weight is important in that it emphasizes the physiological nature of the adjustment to water deficiency. Evidently some forms are able to utilize water or to reduce their rate of water loss more efficiently than others. In a study of the water exchanges of some small mammals, Chew (1951) reported that in Peromyscus, when water drinking was restricted, most of the water conservation which occurred was effected by a reduction in urine volume. Racial differences in ability to adjust to water deficiency when the water was reduced to the same amount for all mice were similar to those observed when the reduction was proportional to the voluntary consumption. It is concluded, therefore, that the ability to maintain weight on a deficiency of water is a characteristic of race.

The most striking differences in adaptation to conditions of varying water deficiency were those between genera. Of all the forms tested, individuals of Perognathus lost the least weight, even though no water at all was provided them. All of these pocket mice in each experiment with deficient water rations survived the entire experimental period. Lindeborg (MS) has subsequently found that Perognathus is able to prevent loss of water through skin and lungs; in completely dry air it lost an average of only 0.80 cc of water per day, whereas Peromyscus leucopus tornillo lost 2.33 cc daily and P. l. noveboracensis slightly more. Perognathus is apparently better adapted for life in an arid habitat than any of the other forms studied.

Microtus showed the least ability to survive on a deficient water supply. Three of 6 individuals failed to survive on 1.8 cc of water daily, while all Peromyscus survived on lesser amounts. When placed on half ration 1 Microtus died, and 2 individuals succumbed on quarter ration. Although none of the races of Peromyscus was able to survive without water, all survived on half ration and only one died on quarter ration. Peromyscus seems to occupy a position intermediate between Perognathus and Microtus in its ability to survive a deficient water supply.

The differences in adjustment to water deficiency exhibited by various races of a given species, though less marked than those between genera, were nonetheless clear. Peromyscus leucopus tornillo not only survived longer on reduced rations than P. l. noveboracensis, but was also able to maintain a higher weight level on all water rations. Likewise, Peromyscus maniculatus blandus survived longer on no water than P. m. bairdi and maintained a higher weight level at each water ration. Within each of the species maniculatus and leucopus, the races which inhabit the more arid regions proved to be somewhat better able to live with reduced water rations than those which inhabit more humid regions.

The correlation between ability to survive on a reduced water supply and occurrence in arid or more humid conditions is also evident in a comparison of forms occupying different habitats in the same geographic region. P. m. bairdi survived longer and maintained a higher weight level than P. l. noveboracensis; in southern Michigan, bairdi lives in grassland which is drier than the woodland habitats occupied by noveboracensis. Likewise, P. eremicus maintained higher weight levels and survived longer than either P. l. tornillo or P. m. blandus; in New Mexico, eremicus lives mainly in rocky situations, blandus in mesquite areas, and tornillo in grassy washes. Eremicus is evidently better adapted to life under conditions of water deficiency than are any other of the forms of Peromyscus tested.

Changes in weather and season must cause considerable variation in the amounts of water available in the habitats of all the mice studied. It has already been shown (Kincer, 1922) that periods of 70 days with less than 0.25 of an inch of rain may occur in southern New Mexico. Perognathus survived for 81 days on air-dry food and no water and would experience little difficulty because of drought conditions. The various Peromyscus races tested could survive extended dry periods. One-half of these mice survived 55 days and some of each race lived at least 66 days on reduced water rations. Periods of 49 days with 0.25 of an inch of rain or less may occur in southern Michigan. One-half of each Peromyscus race tested from this region lived 47 days on reduced water rations and, therefore, could certainly survive extensive seasonal periods of drought. Microtus, however, lived only 22 days on reduced water ration and would find extended dry periods critical to survival.

Lindeborg (1950) has suggested that breeding can take place only when the supply of moisture in the habitat is ample. During the breeding season, nursing bairdi females require more than twice as much water as nonbreeding females. There is a midsummer lull in the breeding activities of this race when temperatures are high and moisture low. It is also possible that subjection to water deficiency while young may be detrimental to future breeding.

In the evolution of races and of species adapted to xeric habitats, mutation and selection of physiologic characters must have played as important a role as that of such morphological characters as dentition, body dimensions, and pelage color. Adjustment of the breeding season to coincide with periods when sufficient water is available to bring the young through to weaning age is an especially important adaptation that presumably is also subject to selection. During its evolution Perognathus p. eremicus evidently developed special physiological adaptations to water deficiency which fit it almost perfectly for life in extremely dry habitats. Microtus p. pennsylvanicus, on the other hand, has not acquired these physiological adaptations to any appreciable degree and is therefore confined to the more mesic habitats. Of the various species of Peromyscus tested eremicus is best adapted to xeric habitats and maniculatus seems to have progressed further in this direction than leucopus.

## SUMMARY

When an abundance of water was supplied under controlled laboratory conditions to adult nonbreeding mice, individual voluntary consumption ranged from no water at all by some pocket mice, Perognathus penicillatus eremicus, to 10.85 cc daily by some voles, Microtus p. pennsylvanicus. The average voluntary consumption by series of individuals was least in Perognathus, greatest in Microtus, and intermediate in the several species and races of Peromyscus tested. Differences in voluntary consumption were greatest between genera, but were also observed between species of the same genus and between races of a given species. A significant difference in water consumption was demonstrated between two stocks of Peromyscus maniculatus gracilis captured in similar habitats about sixty-five miles apart.

When given a water ration less than that consumed voluntarily, all of the forms tested lost weight. Under a reduced water ration, weight is lost rapidly at first, then at a decelerating rate, until a weight level is reached beyond which no further loss occurs. If this regime is continued long enough, individuals of some races may regain weight. All of the forms tested were able to survive on reduced water rations. If the reduction is too severe, however, a mouse may be unable to adjust its physiological requirements to the amount of water received, and it will lose weight steadily until death ensues. The rate of weight loss is dependent on the amount of water provided and on the species and race. Differences in the ability to survive a reduced water ration were also greatest between genera. Individuals of the genus Microtus survived least well on a deficient water ration, whereas those of Perognathus were able to survive on no water at all. The various races of the species of Peromyscus studied likewise differed in their ability to withstand water deficiency.

Within each species of Peromyscus tested the races which consumed least water, when an abundance was provided, and which were best able to survive a reduced water ration were those that naturally live in the more xeric climatic areas. In each climatic area studied, the forms which were better able to survive on deficient water lived in the more xeric habitats. Peromyscus eremicus lived longer and maintained a higher weight level on reduced water rations than any of the other deermice tested; the desert habitats in which this species lives are very arid.

In the evolution of races and species adapted to xeric habitats, selection for the ability to survive a deficient water supply is believed to have played an important role. It is also reflected in the adjustment of breeding season to coincide with periods when sufficient water is available to bring the young through to weaning age. Such physiological characters are as distinctive of taxonomic species and races as are morphological characters.

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